

Chapter 11

Acari

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I. INTRODUCTION

Ecological studies on the soil Acari are changing in character at present. The descriptive approach is no longer an end product, but a basis for analyses of functional relationships between the animals and their environment. This analytical approach includes two distinct, but complementary, lines of enquiry. On the one hand, there are investigations of the structure and behaviour of populations in relation to micro-environmental factors, and on the other, considerations of the effects of these populations on the micro-environment, particularly in relation to the circulation of material and energy through the soil/vegetation system. In simpler terms, this involves a study of action and reaction in a complex community.

The present survey illustrates this change in emphasis and is divided into three main sections. The first recognizes the importance of basic information relating to distribution and population fluctuations. The section on feeding habits underlines the fundamental relationships between soil Acari and their biological environment, and introduces the third section in which the role of soil Acari in the processes of energy transfer and organic decomposition is considered.

The references cited include only those studies directly relevant to the lines of discussion presented. More extensive lists are given by van der Drift (1951) and Kühnelt (1961). This review attempts a synthesis of the more recent developments in the ecology of soil Acari. The fact that more than half of the references cited have appeared during the last 5 years is testimony to the rapid expansion occurring in this field.

II. CLASSIFICATION OF ACARI

Before discussing their ecology, some mention must be made of the general characteristics of the main groups of soil Acari. A comprehensive account of acarine morphology and taxonomy is given by Evans *et al.* (1961); the present account is limited to short, simple definitions to assist the general reader.

Throughout this review the interpretation of acarine classification proposed by Evans *et al.* (1961) is adopted. This system divides the Acari into 7 Orders of which 4, namely the Prostigmata, Mesostigmata, Astigmata and Cryptostigmata, are generally represented in the soil fauna. As their names imply, the adult stages of these groups are distinguished basically on the character of the respiratory system. Unfortunately this is not always easily identifiable and definitions must include other, more readily recognizable structural features. The combination of characters outlined below should

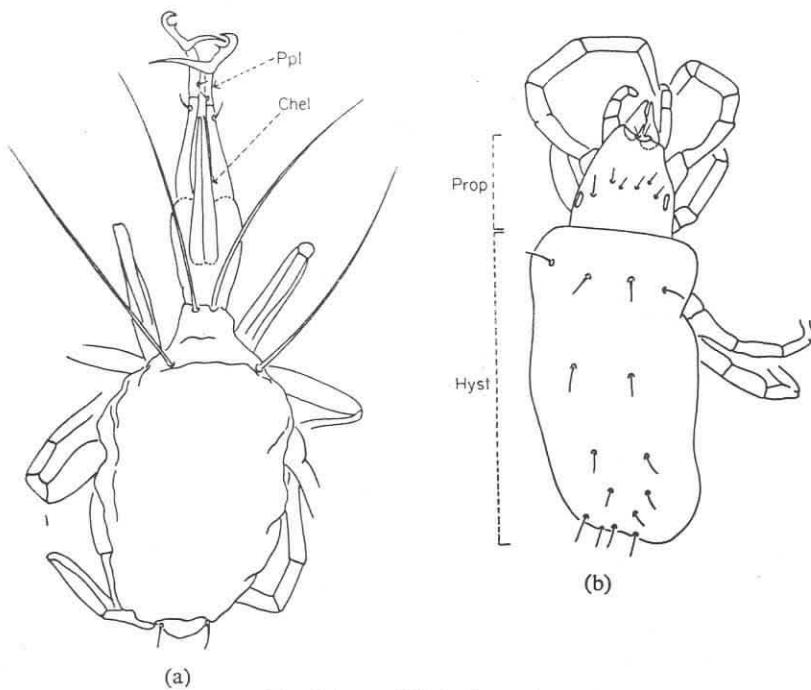


Fig. 1 (see p. 365 for legend)

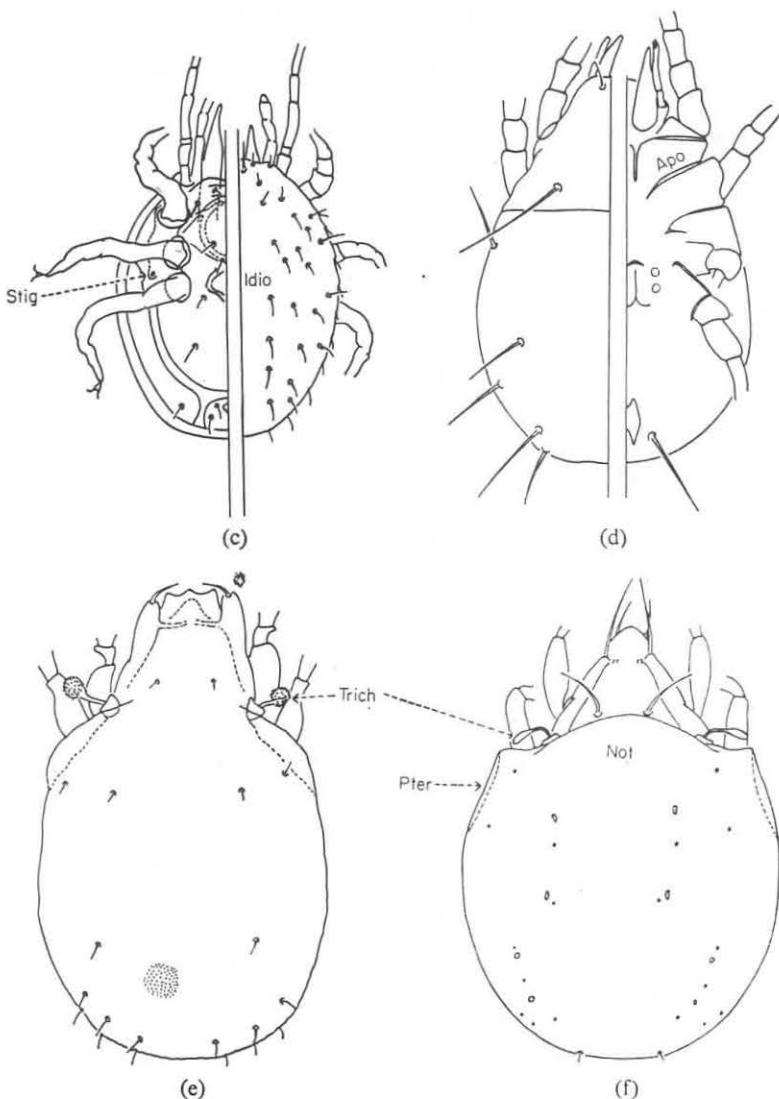


FIG. 1. Representatives of the four orders of soil Acari. (a) Prostigmata, undescribed species from West Africa ($\times 125$). (b) *Rhagidia* sp. (Prostigmata) from Antarctica ($\times 50$). (c) Mesostigmata species, Puerto Rico ($\times 50$). (d) *Rhizoglyphus* sp. (Astigmata) from Britain ($\times 125$). (e) *Tectocephalus* sp. (Cryptostigmata) from Britain ($\times 125$). (f) *Scheloribates* sp. (Cryptostigmata) from Central Africa ($\times 125$).

ppl., pedipalps; chel., chelicerae; prop., propodosoma; hyst., hysterosoma; stig., stigma; idio., idiosoma; apo., coxisternal apodemes; trich., trichobothrium; pter., pteromorph; not., notogaster.

permit the soil ecologist to separate rapidly adult representatives of the Orders encountered.

The Prostigmata is the most variable of the four Orders. Occasionally the tracheal system may be lacking, but it is present in most members of the group, and opens to the exterior by one or two pairs of stigmata located either at the base of the mouthparts (chelicerae) or on the dorsal surface of the anterior region of the body (propodosoma). The mouthparts are usually conspicuous, particularly the chelicerae or "jaws," which may be strong and chelate as in the genus *Rhagidia*, or long and stylet-like. The pedipalps flanking the chelicerae may have a normal palp-like form or may be elongate with a chelate tip (Fig. 1a). The body proper (idiosoma) is often divided by a transverse furrow into an anterior propodosoma and a posterior hysterosoma (Fig. 1b). Both these regions of the body are usually weakly sclerotized, but there are exceptions to this. The propodosoma may bear eyes, and also a maximum of 6 pairs of setae, of which 1 or 2 pairs may have a specialized form (trichobothria). In this Order the trichobothria do not have conspicuous pseudostigmata associated with their insertions.

The tracheal system of the Mesostigmata opens externally by a single pair of stigmata located lateral to the insertions of legs II, III or IV. In all soil species a canal (peritreme), directed forwards, is associated with each stigma. Generally the body is not divided into a propodosoma and hysterosoma (Fig. 1c), although it is covered by one or more sclerotized dorsal plates. The mouthparts are usually housed in a recess (camerostome) at the anterior end of the body. The chelicerae of soil-dwelling Mesostigmata are chelate and can be protruded (Fig. 1c) or retracted within the body cavity.

At first glance, soil Astigmata may be confused with immature Cryptostigmata, for the adults are weakly sclerotized (Fig. 1d). However, they differ from the Cryptostigmata in a number of ways. They lack a tracheal system and stigmata, and the mouthparts are not contained in a camerostome but are exposed and clearly visible from the dorsal aspect. Each pedipalp is reduced to only 2 segments. The body is divided into propodosoma and hysterosoma, although the line of separation is sometimes difficult to see because the integument is weakly sclerotized. Trichobothria are not present on the idiosoma. Conspicuous coxisternal apodemes on the ventral region of the podosoma are also characteristic of the Astigmata (Fig. 1d).

The Cryptostigmata may be identified by the complete or almost complete sclerotization of the body in the adult stage. Propodosomal and hysterosomal divisions are usually present, although there are exceptions to this (Fig. 1e). The propodosoma is covered dorsally by a single plate, the prodorsum, which usually bears sclerotized ridges (lamellae), 4–5 pairs of setae and a pair of trichobothria (pseudostigmatic organs) inserted in specialized pits (pseudostigmata). The hysterosoma is usually covered by a single dorsal plate (notogaster), although sometimes several dorsal sclerites are present. Ventrally, the genital and anal apertures are conspicuous and longitudinal, each covered by a pair of plates. In many groups these apertures are widely separated in a common ventral plate, although in some forms the two regions are

contiguous and flanked respectively by lateral aggenital and adanal plates. A tracheal system is usually present, but stigmata are not conspicuous, being located on the lateral region of the podosoma near the insertions of the legs, or on the legs themselves. The mouthparts are housed in a camerostome and are not exposed in dorsal view, as a general rule. Chelicerae are chelate and the pedipalps are simple and 5-segmented. Many Cryptostigmata show development of lateral notogastral wings or pteromorphs (Fig. 1f), which may or may not be hinged to the notogaster proper.

III. DISTRIBUTION AND DYNAMICS

A. GENERAL DISTRIBUTION OF THE ACARI

Cryptostigmata are numerically the most abundant acarine group in most soils. Many of its members require humidity conditions approaching saturation, and their prevalence in soil compared with more exposed habitats above ground reflects this dependence on high humidity. The Prostigmata and Mesostigmata are usually more active; they range freely through the soil and frequently are not restricted to it. Many of them are predators as, for example, the prostigmatid families Bdellidae, Rhagidiidae, Trombidiidae and the mesostigmatid Veigaiidae, Parasitidae, Gamasolaelaptidae and Macrochelidae. The Astigmata are not important elements in the acarine fauna of many soils, and the role of these mites in the soil community has been little studied. The group is more commonly associated with drier situations where some species such as *Acarus siro* L., *Tyrophagus putrescentiae* (Schrank) and *Tyrolichus casei* Oudms., may become serious pests of stored food products. Intensive studies of various soil communities have shown, however, that Astigmata may be locally abundant in pasture and arable soils. Sheals (1957) recorded *Glycyphagus destructor* (Schrank), *Acarus siro*, *Rhizoglyphus echinopus* (F. & R.) and *Tyrophagus castellanii* (Hirst) from old grassland. Similarly *Caloglyphus mycophagus* (Megnin) and members of the Anoetidae are found in soils where anaerobic decomposition is occurring (Karg, 1963). Most of the qualitative and quantitative information about the ecology of soil acarine populations relates to the European fauna, particularly of Scandinavia, so much of it concerns temperate forest and grassland communities. Because of their numerical abundance, soil Cryptostigmata have been studied more extensively than other soil mites, and much of this section deals with their distribution and population dynamics in temperate soils.

Cryptostigmata occur in greatest numbers in forest soils of the mor type (i.e. in which discrete litter, fermentation and humus layers are present). They are particularly numerous in such soils under oak, beech, Douglas fir, hemlock and pine (van der Drift, 1951; Wallwork, 1959; Crossley and Bohnsack, 1960; Evans *et al.*, 1961), where they may represent as much as 75% of the total acarine fauna. They are less abundant in mull humus formations (i.e. in which mixing of humus and mineral soil prevents the formation of distinct organic layers) such as those developed in grassland, in some forest

soils developed on limestone under oak or beech, for example, and in fenland and heathland soils. However, even under these conditions Cryptostigmata remain the dominant group (Macfadyen, 1952; Sheals, 1957; Engelmann, 1961). Cultivated soils are usually sparsely populated by Cryptostigmata. Although most ecological investigations have been of forest and grassland soils, the communities of other soil and vegetation types such as *Sphagnum* bog and salt marsh have been studied. As a detailed summary of all these ecological surveys would be too exhaustive to be included in this review, mention will be made of a representative selection.

Several species of Cryptostigmata are widely distributed over the North Temperate region, being present in both the Old and the New World. A list of such species includes *Oppia nova* (Oudms.), *Brachychthonius berlesei* Willm., *Tectocephus velatus* (Mich.), *Rhysotritia ardua* (C. L. Koch), *Scheloribates laevigatus* (C. L. Koch), *Platynothrus peltifer* (C. L. Koch), *Ceratoppia bipilis* (Herm.) and *Oribatula tibialis* (Nic.). Similarly in other parts of the world *Malacoangelia remigera* Grandj. appears to have a circum-tropical distribution, *Calyptozetes sarekensis* Trgdh. (Arctic) and *Alaskozetes antarcticus* (Mich.), *Halozetes belgicae* (Mich.) and *Oppia crozetensis* (Richters) (Antarctic) have circum-polar distribution patterns. Despite this fact, many of these species are not ubiquitous in the sense that they occur in every type of soil throughout their geographical range. It is true that some species, for example *Oppia nova*, *Tectocephus velatus* and *Scheloribates laevigatus*, are usually present in a variety of soil conditions from heathland and forest mor to grassland mull [although the last-named species was not recorded from any of 7 forest soils in Britain investigated by Evans (Evans *et al.*, 1961)]. More often, however, species are much more limited in their distribution, as shown when faunal comparisons between communities reveal variations in species composition. These variations occur not only between communities of different vegetational types such as heathland, bog, grassland and forest, but also on a more restricted scale as, for example, between different forest soils. Thus, in the above-mentioned study by Evans, of the 67 species of Cryptostigmata recovered from 7 forest soils, 26 species were restricted to one or other of these soils. A survey made on two adjacent pastures in Kentucky, one grazed by sheep and the other by cattle (Wallwork and Rodriguez, 1961), revealed 13 species of Cryptostigmata from sheep pasture compared with only 8 from cattle pasture; furthermore the dominant species in sheep pasture were *Galumna virginiensis* Jacot and *Scheloribates laevigatus*, whereas in cattle pasture *Eupelops* sp. was dominant. Studies such as these suggest that micro-environmental factors may affect considerably the species composition of the acarine component of a soil community. Pronounced variations occur when soil Acari from different edaphic and vegetational conditions are compared. Thus *Steganacarus magnus* (Nic.), *Nothrus sylvestris* (Nic.), *Carabodes labyrinthicus* (Mich.), *Fuscozetes fuscipes* (C. L. Koch), *Phthiracarus borealis* (Trgdh.) and *Mesophlophora pulchra* Selln. are more commonly associated with highly organic deposits in forest soils. Species and individuals of Galumnidae are frequently

less common in forest soils than in grassland soils; other species associated with the latter are *Oppia minus* (Paoli), *Puncoribates punctum* (C. L. Koch), *Ceratozetes gracilis* (Mich.) and small forms belonging to the genera *Brachychthonius* and *Suctobelba*. However, such characterizations are by no means exclusive and, if anything, tend to oversimplify the natural relationships between the species and its environment.

B. SYNECOLOGY

In an attempt to relate species composition to micro-environment Strenzke (1952) proposed to define groups of species (Synusien) whose distribution is a function of their dependence on a particular combination of micro-environmental factors (moisture content, organic content, pH, salinity, ground cover). The suggestion that certain species always occur with certain other species or their ecological equivalents is implicit in this concept, and has been demonstrated for certain communities (Klima, 1959). However, its general applicability remains to be established. Rajska (1961) investigated the Cryptostigmata of 5 plant associations in the vicinity of Poznan and concluded that a number of synusiae could be defined, namely syn. *Hydrozetes lemnae*, *Ceratozetes mediocris*, *Nanhermannia comitalis*, *Damaeus riparius* and *Chamobates borealis*. These groups apparently represented a community succession paralleling that of the vegetation during the transition from a purely aquatic (fresh-water) condition through meadow to deciduous woodland. Community succession in a *Sphagnum* bog has been studied by Tarras-Wahlberg (1954, 1961) with the definition of a characteristic association of species including *Tectocepheus velatus*, *Malacothrus gracilis* van der Hammen, *Nanhermannia nana* (Nic.) and *Nothrus pratensis* Selln. in the hummocks. Hammer (1937) recognized a *Platynothrus peltifer*/*Melanozetes* sp. community in east Greenland characteristic of wet biotopes (lake bank, bog and moss) and a dry biotope community (fell-fields, heath and grassland) characterized by *Zygoribatula exilis* (Nic.), *Calyptozetes sarekensis* and *Camisia horrida* (Herm.). Haarløv (1942) was able to identify the wet biotope community but not the dry one in north-east Greenland. The fact that such findings may be valid only within a limited geographical area emerges if they are compared with those of Weis-Fogh (1948) from Denmark, who described a wet or moist biotope characterized by *Tectocepheus velatus* and *Scheloribates laevigatus* and a dry community with *Folsomia quadrioculata* (Collembola) and *Variatipes quadrangularis* (Berl.) (Prostigmata) as the characteristic groups. The findings of Forsslund (1943), Karppinen (1955, 1958), Knüllé (1957) and Klima (1959) are examples of many similar studies.

The definition of various communities having characteristic species has stimulated attempts to assess the extent of the similarity between them. Several statistical methods are available for this purpose, each of which has its disadvantages. One of the most commonly used is that based on "quotients of similarity" (Franz, 1963). The limited usefulness of the sociological approach has been discussed by Haarløv (1960). Evidently some species can be

used as indicators of special environmental conditions. *Platynothrus peltifer*, *Nothrus palustris* C. L. Koch and *Hydrozetes* spp. are associated with wet or moist biotopes; *Pelops acromios* (Herm.), *Phauloppi lucorum* (C. L. Koch), *Dometorina plantivaga* (Berl.), *Pirnodus detectidens* Grandj., *Mycobates parmeliae* (Mich.) and *Camisia horrida* are more common in dry localities (Travé, 1963). Despite these examples, a large number of Cryptostigmata such as *Tectocepheus velatus*, *Scheloribates laevigatus* and *Oppia nova* will tolerate a wide range of ecological conditions and are therefore poor indicators. This is well illustrated by a study of the zonation of Cryptostigmata in 4 alpine vegetation zones in Sweden (Dalenius, 1962). Of the 76 species recorded from all zones, the greatest number (67) occurred in the vegetation belt below the timber line, but more than half of these also occurred in vegetation belts above the timber line. This study contrasts with that of Evans discussed earlier and illustrates the difficulty of making broad comparisons. Only in restricted habitats having a small number of species, such as the intertidal zone, can strong associations be recognized.

C. VERTICAL DISTRIBUTION

The vertical distribution of Acari is well documented and it is generally recognized that species composition varies with depth in the soil. Three distinct ecological zones can be distinguished in any vegetation type, namely (1) the epigeal zone (vegetation zone), (2) hemiedaphic zone (organic layers associated with the surface of the soil) and (3) the euedaphic zone (the deeper mineral strata of the soil). Soil Acari are primarily hemiedaphic, although their distribution may also extend into the other two zones, as with active and tolerant species. Thus, many predatory Prostigmata and Mesostigmata may be found in all three zones; some tolerant Cryptostigmata, such as *Passalozetes* spp., *Scutovortex* spp., *Oribatula tibialis* (Nic.) and *Eremaeus* spp., may be similarly distributed. Again, a number of hemiedaphic species such as *Galumna virginiensis*, *Scheloribates laevigatus*, *Eupelops* spp. and *Diapterobates humeralis* (Herm.) show regular vertical movements into and from the epigeal zone (Wallwork and Rodriguez, 1961; Tarras-Wahlberg, 1961). This activity seems to be correlated with the humidity fluctuations of the epigeal zone. On the other hand, the hemiedaphon is itself heterogeneous and may be sub-divided into the organic strata lying on the surface of mineral soil and the more specialized habitats associated with moss, lichens and bark. Here also, faunal division is largely arbitrary for there is considerable overlap in species distribution (Travé, 1963). The form of the organic deposits in soil influences distribution. A fairly even vertical pattern may be found to a depth of 20 to 30 cm in a mull grassland soil where humus material mixes extensively with mineral soil. In contrast, the fauna of a heath or forest mor is very largely concentrated in the surface organic layers which may vary in total thickness from 1 to 8 cm (Murphy, 1955).

Cryptostigmata in forest soils are usually most numerous in the fermentation layer or, when this is not defined, in a zone of intergradation between

litter and humus. The upper parts of litter are frequently subject to extremes of temperature and to desiccation which undoubtedly limit acarine distribution in this region. Deeper organic layers rarely dry out, for even when the moisture decreases appreciably the relative humidity within the soil cavities remains high (Thamdrup, 1939). In these lower layers the diameter of the soil interstices may limit depth distribution of soil Acari. These cavities become smaller with increasing depth (Haarløv, 1960), and as most soil Acari move through these channels it is not surprising to find smaller species becoming relatively more abundant with increasing depth. Some medium- and small-sized species show little or no decided preference for one or other of the organic strata and are frequently found in all layers, except perhaps the upper litter layer. Such species include *Scheloribates laevigatus*, *Oppia nova*, *Suctobelba* spp., *Tectocepheus velatus* and *Brachychthonius* spp. Species showing a preference for the litter layer include the large predatory and trachytoid Mesostigmata and the cryptostigmatid species *Platynothrus peltifer*, *Oribatula tibialis*, *Chamobates* sp. and *Achipteria coleoptrata* (L.) (van der Drift, 1951; Wallwork, 1959; Evans et al., 1961). Many more prefer the more stable conditions of the lower litter layer and the zone of intergradation between litter and humus. Typical of this region are *Hypochthonius rufulus* (C. L. Koch), *Nanhermannia* spp., *Nothrus silvestris*, *Oppia ornata* (Oudms.), *Phthiracarus borealis*, *Rhysotritia* spp., *Belba* spp. and members of the mesostigmatid families Zerconidae and Digamasellidae. Examples of the few species which prefer the humus layer proper are *Rhysotritia minima* (Berl.), *Rhysotritia ardua* (C. L. Koch), *Suctobelba sarekensis* Forssl. and *Oppia minus*. Deeper still in the lower layers of the humus and in underlying mineral soil *Rhodacarus* sp. (Mesostigmata), small *Oppia* species and immature forms occur sporadically. There is little food in the deeper mineral layers and consequently the fauna is impoverished.

It must be remembered that these distribution patterns are not static. Vertical movements occur between one organic stratum and another, and are obviously more frequent among the active predatory Prostigmata and Mesostigmata than among the more sedentary Cryptostigmata. Nevertheless this activity may also be characteristic of many Cryptostigmata. The diurnal movements of some species between the hemiedaphon and epigeal zone have been mentioned already. Similar short-term movements between different organic layers in the hemiedaphon also occur (Tarras-Wahlberg, 1961) and these may be responses to less favourable temperature conditions in certain parts of the profile. Recent work by Berthet (1964) shows that some of the larger Cryptostigmata may move appreciable distances daily, and that sometimes these movements are positively correlated with the moisture content of the litter. This suggests that such behaviour is at least partly controlled by environmental factors. The more thoroughly studied seasonal movements are probably governed in much the same way and may be regarded as long-term extensions of the diurnal phenomenon. On the other hand, seasonal movements may have an antagonistic effect on diurnal movements. Populations normally moving between surface and deeper layers during the diurnal

cycle in summer may be restricted to deeper layers during winter and show little or no diurnal vertical movement during this season. This will depend, to a great extent, on local conditions such as the amount of snow cover and temperature variations within the soil profile. In temperate soils the larger species such as *Platynothrus peltifer*, *Oribatula tibialis*, *Chamobates* sp. and *Achipteria coleoptrata* which prefer the litter layer apparently maintain this preference throughout the year, even during hot and cold dry periods, and evidently can tolerate these unfavourable conditions (van der Drift, 1951; Wallwork, 1959). *Nothrus silvestris*, *N. pratensis*, *Scheloribates laevigatus*, *Oppia nova* and many of the medium and smaller forms normally found in litter and fermentation layers during the summer decrease in numbers in these layers during winter, in some localities. This decrease is frequently associated with an increase in numbers in humus and such circumstantial evidence suggests a downward movement from litter to humus during early winter. Van der Drift (1951) and Karppinen (1955) attribute this movement to an avoidance of the dry, cold conditions in litter at this time. Experiments on the temperature preference of *Oppia nova* also support this view (Wallwork, 1960). Lebrun (1964b) has reservations regarding the smaller species, for he could detect no downward movement into the humus layer of an oak mull forest floor at the onset of winter in the species *Suctobelba subtrigona* (Oudms.), *Oppia quadricarinata* (Mich.), *O. ornata*, *O. subpectinata* (Oudms.), *Autogneta willmanni* (Dyrd.), *Tectocepheus velatus* and *Minunthozetes semirufus* (C. L. Koch). Clearly these behaviour patterns can only be explained in the context of the natural conditions to which the particular animals are accustomed. The findings from one locality do not necessarily apply generally, particularly for ecologically tolerant species. Much has still to be learned about the physiological basis of behaviour in the Acari. Experimental work on temperature preferences (Wallwork, 1960; Tarras-Wahlberg, 1961) indicates that various species differ in their reactions to certain temperature conditions, and that these reactions are governed in part by the environmental temperature range naturally encountered by the species. Investigations of humidity preferences have produced similar results (Madge, 1964a, b); thus, litter-dwelling species *Platynothrus peltifer* and *Belba geniculosa* Oudms. showed a preference for high humidity under experimental conditions, whereas *Humerobates rostrolumellatus* Grandj., an arboreal species, initially preferred a low humidity but reversed this response after one-third the initial body weight was lost. These responses are affected by the amount of water in the body and the nutritional state of the animal.

D. LIFE FORMS

Morphological adaptations of certain species to particular ecological zones may lead to the definition of life forms. The correlation between body size and depth distribution, where the diameter of the soil interstices is a limiting factor, has been discussed above. Soil porosity is by no means the only limiting factor in the distribution of soil Acari, and other morphological

features associated with improved locomotion and reduction of water loss across the integument have been considered as direct adaptations to particular environmental conditions. Klima (1956) correlated body width of various Cryptostigmata with vertical distribution in the soil, and also considered (1) the functional relationship between the structure of the integument and resistance to desiccation and (2) the colour of the body and the amount of light to which the species is naturally exposed. These correlations formed the basis for a definition of structural classes whereby the species concerned were grouped into euedaphic, hemiedaphic (with its hygrophilous, mesophilous and xerophilous subdivisions distinguished) and epigeal (atmobios) forms. Tarras-Wahlberg (1961) devised similar groupings for the Cryptostigmata from a bog by correlating the form of the pseudostigmatic organ with the environmental moisture gradient. Thus, hygrophilous species such as *Limnozetes ciliatus* (Mich.) and *Trimalaconothrus novus* Selln. have greatly reduced pseudostigmatic organs; in xerophilous and epigeal species such as *Carabodes labyrinthicus*, *Scheloribates laevigatus* and *Phauloppia lucorum* these organs are globular, whereas in the mesophilous species a wide variety of form exists. Reduction of sensillae is quite common among aquatic and semi-aquatic (fresh-water and inter-tidal) Cryptostigmata belonging to the genera *Hydrozetes*, *Ameronothrus*, *Hygroribates* and *Halozetes*. It must be remembered, however, that even in these conditions there are many species which do not appear to be morphologically adapted (Luxton, 1964). This may reflect a lack of knowledge concerning the sensory physiology and behaviour of Acari. The difficulty in applying the concept of life forms to soil Cryptostigmata has been stressed by Märkel (1964) in a study of species distribution in three different sites. Horizontal and vertical distribution of three species associations, *Rhysotritia duplicata*, *Steganacarus spinosus* and *Hermannia gibba*, differed from site to site and appeared to be governed by distribution of food rather than by physical characteristics of the environment.

E. POPULATION FLUCTUATIONS AND PHENOLOGY

Unlike the Mesostigmata and, to a lesser extent, the Prostigmata, soil Cryptostigmata show seasonal fluctuations in population size and age class distribution. Detection of these population changes depends, ultimately, on the efficiency of sampling. Variations in counts occur within series of samples and partly result from the non-random distribution of soil mites. Reliable estimates of population density can be achieved, however, by assessing statistically the degree of aggregation and analysing the sources of variation (Macfadyen, 1952; Hartenstein, 1961; Healy, 1962; Ibarra *et al.* 1965). Population fluctuations are closely related to the length of the life cycle and the number of generations per year of the constituent species. These are influenced in turn by environmental conditions, so that broad geographical variations in fluctuation patterns may be expected. Hammer (1944) recorded maximum populations of mites and Collembola in Greenland during the summer, at a time when temperate mite populations are at a minimum. Unfortunately

there is little information about fluctuations in tropical soils where precipitation may be an important factor.

In general, populations of *Cryptostigmata* in the European and North American habitats studied are greatest during the autumn and winter months (October to February) and least during the summer (July to August). This applies to forest soils (Evans, 1955; Wallwork, 1959), fenland soil (Macfadyen, 1952) and uncultivated grassland (Sheals, 1957) with only minor variations depending on variations in local climatic conditions (Fig. 2). The autumn/winter population peak is largely produced by the appearance of larval and protonymphal stages; adults are generally more abundant during late

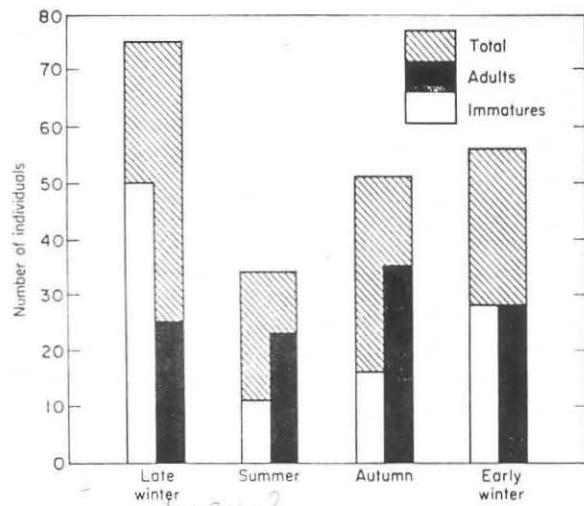


FIG. 2. Seasonal fluctuations in density and age class distribution of the *Cryptostigmata* of a hemlock-yellow birch forest floor at Imp Lake, Michigan, U.S.A.

summer and early autumn when, presumably, the eggs are laid from which winter immatures will develop. This would certainly seem to be true of the humus populations and because many litter-dwelling species move down into humus at the onset of winter, changes in humus populations at this time will form a significant part of the total population change in the profile as a whole. However, a small number of species live predominantly in the litter throughout the year. In contrast to those in humus, litter populations of these species evidently are greatest in spring and early summer (Lebrun, 1964a). Furthermore, the life cycles of all species are not synchronized; one, two or even three generations may be produced in a year, depending on the species and the climatic conditions. Observations on laboratory cultures have demonstrated that the life cycles of many *Cryptostigmata* are relatively long (Grandjean, 1950; Pauly, 1956; Sengbusch, 1958). Lebrun (1964a) combined this approach with age class distribution data from samples of field populations

to determine the phenology of Cryptostigmata, taking account of climatic factors and species tolerance. He suggested that *Nothrus silvestris*, *Chamobates incisus* van der Hammen, *Rhysotritia ardua* (C. L. Koch), *Platynothrus peltifer* and *Euzetes globulus* (Nic.) have only one generation per year, whereas *Oppia nova*, *Autogneta willmanni*, *Nanhermannia elegantula* Berl., *Steganacarus magnus*, *Minunthozetes semirufus*, *Parachipteria willmanni* van der Hammen, *Phthiracarus piger* (Scop.) and *Damaeus onustus* C. L. Koch, may have two generations per year under the same conditions. *Carabodes marginatus* (Mich.), *Chamobates cuspidatus* (Mich.) and *Oribatella quadricornuta* (Mich.) are examples of species which could produce 3 generations per year. *Tectocephalus velatus* and *Oppia subpectinata* are also included in the latter group for they are highly adaptable to local conditions, and may produce 3–5 generations per year when conditions are favourable. They may also produce fewer than this, for Haarlev (1960) and Murphy and Jalil (1964) have suggested two generations per year for *T. velatus*. Under more exacting climatic conditions, such as the long, cold winters and hot summers occurring in parts of North America, most species may produce only one generation per year, as indicated in Fig. 2.

IV. FEEDING HABITS

An understanding of the feeding habits of soil Acari is necessary before the role of these organisms in the energetics of the soil community can be analysed critically. Soil presents a large and varied assortment of ecological niches and it is not surprising that the Acari show a corresponding variety of feeding habit. The extent to which Acari exploit these niches is still not fully known, largely through lack of information about natural feeding habits. Attention has been focused on this problem in recent years, and whereas much has been learned from studies on laboratory cultures, these observations cannot be applied indiscriminately to field populations. Generalizations based on the structure of mouthparts must also be treated cautiously. Direct observation of natural feeding activity is difficult because of the small size of the mites and their cryptic behaviour, although the habits of some Acari, such as wood-boring Cryptostigmata, make this possible. In most instances reliable information on feeding habit is obtained from gut content analyses of large samples taken directly from the field. Information can be obtained from such analyses by using differential staining techniques to identify lignin, cellulose and chitin components. The more conspicuous fungal hyphae and spores can be identified without staining (Fig. 3). Occasionally it is possible to determine feeding habit by identifying characteristic lesions in litter fragments. This method has been used to discriminate between the feeding activity of Diptera larvae, earthworms and small arthropods on small litter samples (Edwards and Heath, 1963). It may also be applied to leaf- and wood-boring mites, although it is unlikely that it could be used generally at the specific level for soil-inhabiting forms.

The feeding habits of selected groups of soil Acari are given in Tables I

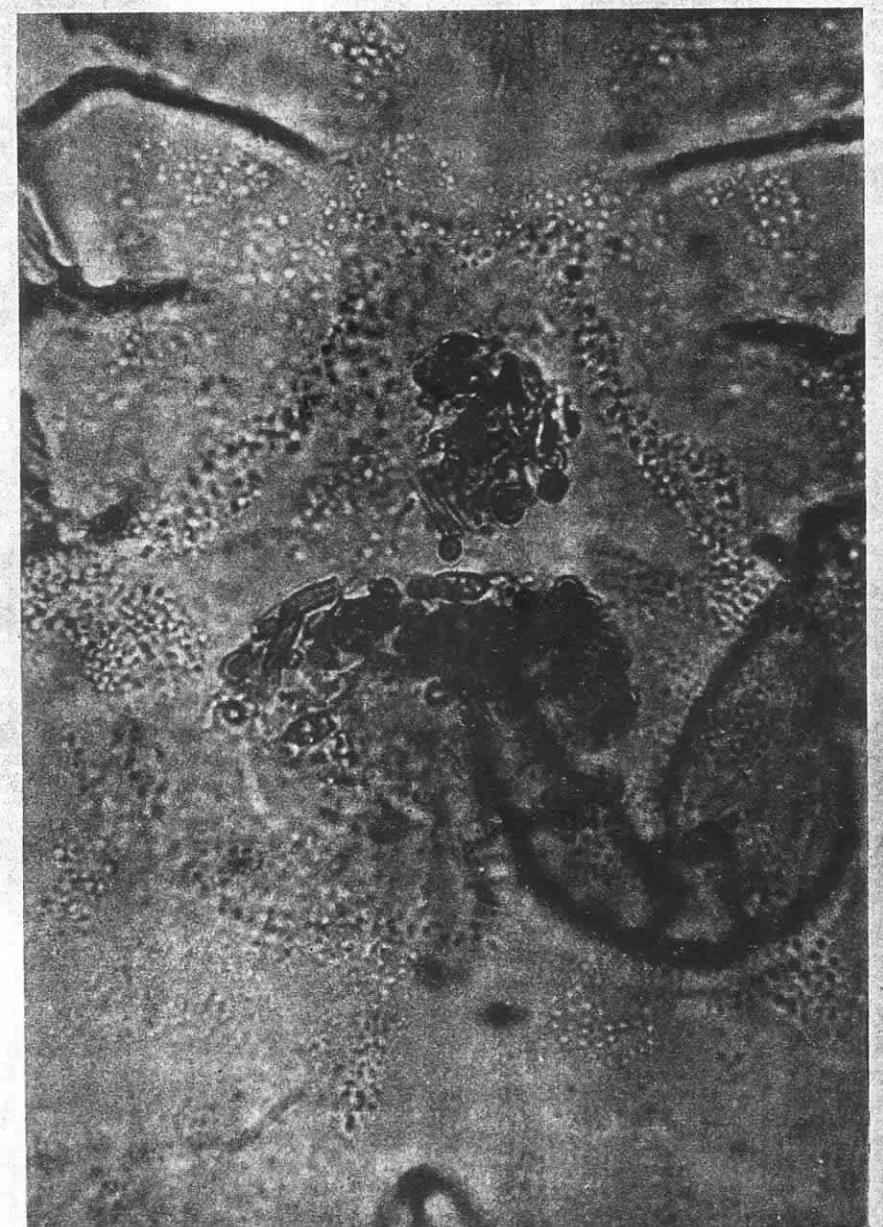


FIG. 3. Contents of the mid-gut of a cryptostigmatid tritonymph taken on Macquarie Island. Fungal spores and hyphae surrounded by a fluid or semi-fluid material can be identified ($\times 500$).

TABLE I

The feeding habits of selected groups of soil Acari belonging to the orders Prostigmata, Mesostigmata and Astigmata*

Group	Carnivore		Herbivore/Decomposer			
	Predator		Plant detritus	Moss and lichens	Wood	Fungi and algae
Prostigmata						
Bdellidae	x					
Trombidiidae	x					
Tydeidae	(x)					x
Rhagidiidae	x					
Eupodidae	(x)					(x)
Erythraeidae						
<i>Erythraeus</i>	x					
<i>Balaustium</i>	x		x			
Scutacaridae	(x)					x
Pyemotidae						x
Tarsonemidae						x
Mesostigmata						
Macrochelidae	x					
Veigaiidae	x					
Parasitidae	x					
Zerconidae	(x)		x		x	x
Digamasellidae	(x)					
Uropodidae						
<i>Uropoda</i>			(x)			
<i>Fuscuropoda</i>	x		x			(x)
Trachytidae			x			x
Rhodacaridae	(x)					
Astigmata						
Glycyphagidae						x
Acaridae						
<i>Histiogaster</i>				(x)		x
<i>Rhizoglyphus</i>			x			(x)
<i>Schwiebea</i>				(x)		(x)
<i>Caloglyphus</i>						(x)
Anoetidae		x				x

* Symbols in parentheses denote unconfirmed or conflicting reports.

and II. As information on feeding behaviour accumulates it is becoming more difficult to generalize about these habits at the familial, generic and specific levels, and consequently several different kinds of behaviour may occur within these levels. The soil-dwelling Prostigmata and Mesostigmata are largely represented by predatory forms. Astigmata feed mainly on liquids or plant detritus in an advanced stage of decomposition in the soil. Cryptostigmata have generally been considered as fungal feeders, although the data

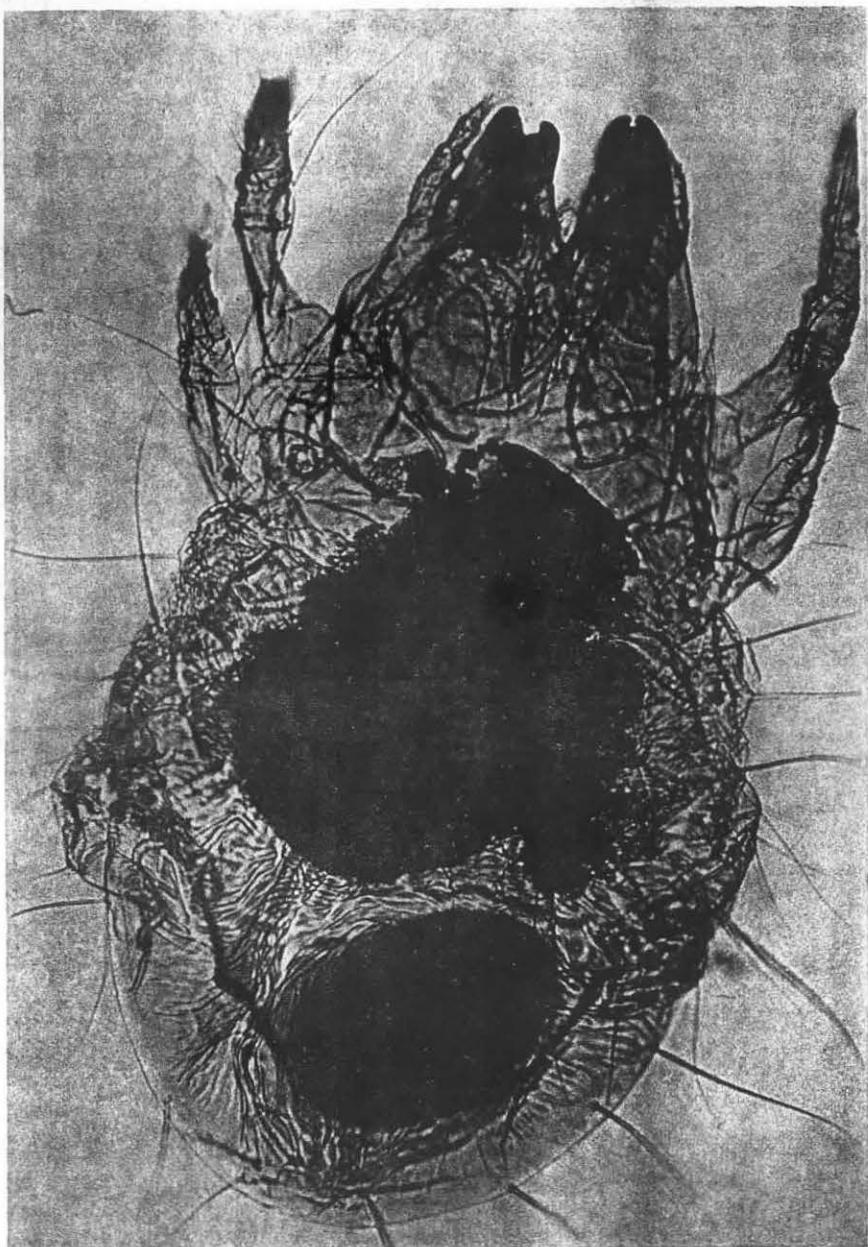


FIG. 4. Tritonymph of a cryptostigmatid mite (*Hermannia* sp.?) taken from lenticel of fallen yellow birch twig at Imp Lake, Michigan, U.S.A. Black cork material from the lenticel is present in the gut ($\times 125$).

given in Table II indicate a wide range of feeding habit. Each of these groups will be considered separately.

A. PROSTIGMATA

Predatory Prostigmata, with their stylet-like mouthparts adapted for piercing and sucking, probably form an important trophic link in the soil community between soft-bodied Astigmata and immature Cryptostigmata on which they feed, and the larger carnivorous arthropods. Predatory activities of a number of common families, such as the Bdellidae, Cheyletidae, Rhagidiidae and Trombidiidae, are well established (Baker and Wharton, 1952). The Tydeidae have also been considered as predators on eggs and small arthropods in the soil (Baker and Wharton, 1952), although Karg (1963) was not able to observe predatory activity in cultures and concluded from his observations and examinations of mouthparts that they are fungal feeders. Some confusion surrounds the feeding habits of the Eupodidae. Kühnelt (1961) considers them to be mainly predatory, whereas Evans *et al.* (1961) suggest that they are fungal feeders. The family contains a number of phytophagous species which are agricultural pests in certain countries (Baker and Wharton, 1952). Very little is known of the feeding of some of the smaller soil-dwelling prostigmatids such as the Scutacaridae, Pyemotidae and Tarsonemidae. Many of them may be introduced accidentally into the soil by other invertebrates, for they are known to be parasitic or phoretic on larger arthropods, such as insects. They are considered to be fungal feeders, although they may occupy a niche similar to that of the phoretic Mesostigmata, such as *Macrocheles muscaedomesticae* (Scop.), which feed on insect eggs and small nematodes. The family Erythraeidae contains aggressive predators, common examples of which belong to the genera *Erythraeus* and *Balaustium*. In contrast to other Erythraeidae the genus *Balaustium* has a wide range of feeding habit (Newell, 1963), some species being active predators of scale insects, thrips and other insects associated with vegetation, others being phytophagous on green leaves or on pollen.

B. MESOSTIGMATA

Many of the predatory Mesostigmata are large, active mites with mouthparts adapted for piercing, sucking and tearing (Figs 5 and 7). Representatives of the genera *Veigaia*, *Pergamasus*, *Parasitus*, *Gamasolaelaps* and *Macrocheles* are commonly present in many forest soils. *Veigaia* spp. are known to feed in culture on proturans, collembolans and pauropods (Huflbutt, 1964), and have also been observed to attack cryptostigmatid mites (Wallwork, 1957). *Veigaia mitis* (Berl.) feeds by piercing the integument of the prey, inserting the two chelicerae which move forwards and backwards simultaneously or alternately, and imbibing the body fluids. The action of the chelicerae probably serves to macerate the body tissues of the prey and also to assist in the imbibition process. Some of the large, viviparous mesostigmatids, such as *Pergamasus* spp., feed on their own young in culture, in

addition to Collembola, insect larvae and the nymphs of *Parasitus* sp. and *Gamasolaelaps* sp.. The genus *Macrocheles* is frequently found in rather specialized habitats, such as dung and compost, where its members live phoretically with certain Diptera and Coleoptera. *M. muscaedomesticae*, phoretic on the house fly, feeds on eggs and first-instar larvae of this dipteran.

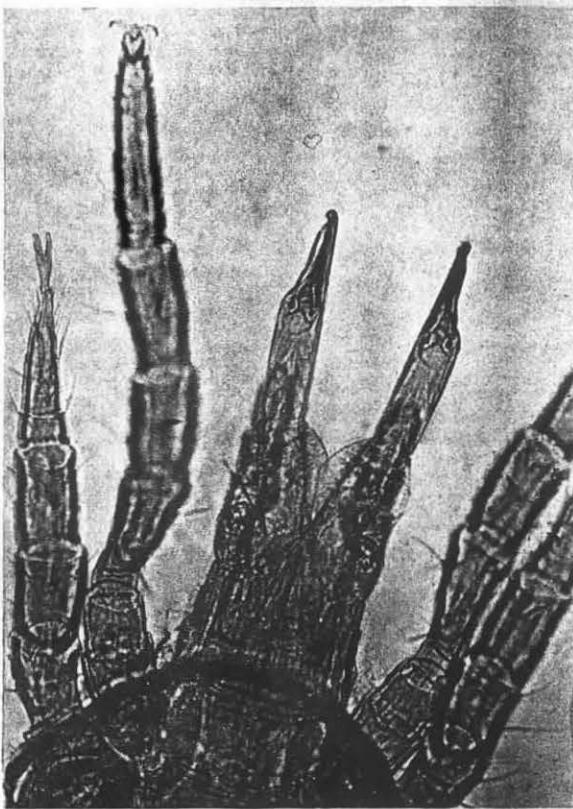


FIG. 5. Mouthparts of a predatory mesostigmatid mite from Puerto Rico (specimen from collection of Dr. Maldonado Capriles) ($\times 125$).

Wallwork and Rodriguez (1963) have demonstrated that the feeding rate of this mite is related to the amount of ammonia in the substrate, and that the feeding response (i.e. puncturing of eggs) will continue as long as the concentration of ammonia remains above a threshold, despite the fact that the mite may be completely engorged. This species has also been shown to feed on the nematode *Rhabditella leptura*, Collembola and various Astigmata. It is probable that these organisms, together with insect eggs, form the diet of at least some of the macrochelids of pasture and forest soils. The Zerconidae and Digamasellidae may be predators (Wallwork, 1957), although small



FIG. 6. High power view of the cerotegument of tritonymph of *Halozetes* sp. (Cryptostigmata) from Macquarie Island, showing diatoms adhering to body surface ($\times 500$).

in size and less active than the larger forms. More information is needed on their feeding habits. Many of these predatory forms are also considered to be carrion feeders (Kühnelt, 1961), but this requires confirmation. Another group of Mesostigmata, the Uropodina, contains a number of fungal-feeding mites (Evans *et al.*, 1961). These are slow moving and not adapted to a predatory habit, although one member of this group, *Fuscuropoda marginata* (C. L. Koch), which has been considered coprophagous (Kühnelt, 1961), has been shown to be a predator of the astigmatid mite *Caloglyphus mycophagus* (Rohde, 1959).

C. ASTIGMATA

The feeding habits of the soil-dwelling members of this group of mites are not well known, although it is probable that they feed on plant detritus, fungi, algae and the liquified products of putrefaction processes (Karg, 1963). The Glycyphagidae are mainly fungal feeders, and the same appears to be true of the *Histiogaster* species found in the galleries of wood-boring beetles. Members of this last-named genus apparently have a wide range of feeding habit, and have also been recorded as carrion-feeders (Woodring, 1963), a habit also shown by the anoetid genus *Histiosoma*. Karg (1963) considers many of the Anoetidae to be filter feeders on liquids rich in micro-organisms. As far as other soil-dwelling species are concerned, *Rhizoglyphus* species feed on decaying plant material, *Caloglyphus* species on carrion, although they may also be fungivorous; *Schwiebia talpa* Oudms. has been recovered from beneath the bark and in cavities in hemlock and yellow birch twigs lying on the forest floor (Wallwork, 1957), and although the feeding habits of this species have not been established with certainty, it may feed on fungi and the woody products of fungal decay in this situation. In general, it would seem that soil Astigmata require for their maintenance organic material in an advanced stage of decay, low oxygen concentration, and a plentiful supply of moisture.

D. CRYPTOSTIGMATA

Cryptostigmata may be an important element in the decomposer food-chain in the soil community on account of their feeding habits. Many species feed on soil fungi and bacteria and it has been suggested that the mites may control the growth of these organisms (Engelmann, 1961). Evidently the relationship is not a simple one, for mites also help to disseminate fungal spores. A great many Cryptostigmata are unspecialized feeders, and indeed, restriction to one type of food is rare in these soil forms. The emphasis hitherto placed on fungal food arises partly because hyphae and spores are easily identified in gut contents, whereas plant material in an advanced stage of decomposition is not. Results of feeding experiments made by Hartenstein (1962) on 20 species indicate that about half of them preferred fungi as food, whereas the others preferred decomposing plant material. This lack of specificity of many species has been noted commonly in observations on cultures



FIG. 7. Cheliceral digits of *Gamasolaelaps* sp. (Mesostigmata) ($\times 500$).

TABLE II
The feeding habits of selected groups of soil Cryptostigmata

Group	Herbivore		Decomposer		Microphyte	
	Green plants	Plant detritus	Wood	Carrion	Moss and lichen	Fungi and algae
<i>Hypochthonius</i>				x	x	x
<i>Liochthonius</i>	x			x		x
<i>Eniochthonius</i>	x					x
<i>Camisia</i>	x				x	x
<i>Nothrus</i>						
<i>silvestris</i>	x				x	x
<i>palustris</i>					x	
<i>Platynothrus</i>	x					
<i>Nanhermannia</i>	x				x	x
<i>Mesoplophora</i>						
<i>pulchra</i>			x			x
<i>Pthiracarus</i>	x	x				x
<i>Steganacarus</i>						
<i>magnus</i>	x		x			
<i>Rhysotritia</i>						
<i>ardua</i>	x		x			
<i>Euphthiracarus</i>					x	
<i>Hermannia</i>	x		x			
<i>Liacarus</i>	x		x			x
<i>Adoristes</i>						
<i>ovatus</i>	x					x
<i>Ceratoppia</i>			x			x
<i>Hermannella</i>	x		x			
<i>Carabodes</i>	x		x			x
<i>Cepheus</i>			x		x	
<i>Tectocepheus</i>						x?
<i>velatus</i>	x					x?
<i>Belba</i>	x			x		x
<i>Oppia nova</i>	x				x	x
<i>Oppia</i> spp.			x			x
<i>Oribatula</i>						
<i>tibialis</i>						x
<i>Scheloribates</i>	x	x	x		x	x
<i>Achipteria</i>	x	x			x	x
<i>Fuscozetes</i>						
<i>fuscipes</i>	x					x
<i>Peloribates</i>	x	x	x	x		x
<i>Protoribates</i>	x		x			
<i>Ceratozetes</i>	x		x			x
<i>Eupelops</i>	x	x				
<i>Galumna</i> (s.l.)	x	x	x		x	x

and gut contents (Forsslund, 1939; Riha, 1951; Schuster, 1956; Wallwork, 1957; Woodring and Cook, 1962), and is illustrated by data presented in Table II.

Some tentative conclusions may be drawn from these findings. Species

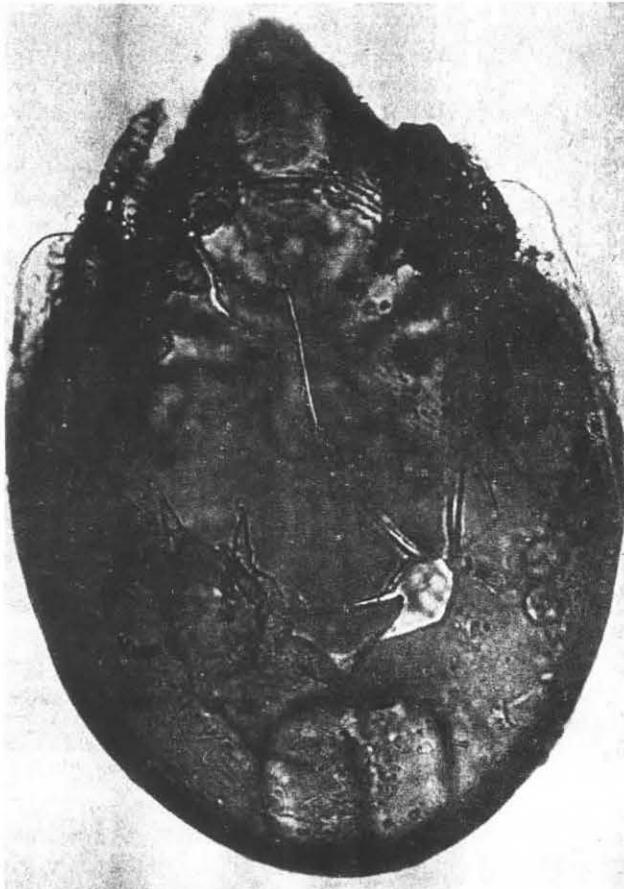


FIG. 8. *Scheloribates perforatus* Wallw. showing development of larva inside shell of the adult ($\times 125$).

predominantly fungivorous under natural and artificial conditions include *Ceratoppia bipilis* (Herm.), *Adoristes ovatus* (C. L. Koch), *Belba* spp., *Belba kingi* Hartenstein, *Oribatula tibialis*, *Oribatula minuta* (Banks), *Scheloribates laevigatus*, *Ceratozetes gracilis* (Mich.) and *Galumna elimata* (C. L. Koch). Sustained feeding on plant fragments will only occur, generally, if these fragments are undergoing wet decomposition. Such food material is suitable

for many Cryptostigmata including *Liochthonius* sp., *Nothrus silvestris*, *Nothrus biciliatus* (C. L. Koch), *Platynothrus peltifer*, *Camisia* spp., *Phthiracarus* spp., *Hermannia* sp., *Liacarus xylariae* (Schränck), *Carabodes* spp., *Oribatella* sp., *Fuscozetes fuscipes* (C. L. Koch), *Peloribates* sp., *Protoribates lophotrichus* Berl. and *Eupelops* sp. Feeding preference is frequently related to the stage of decomposition of the plant material. Thus, *Achipteria* sp. will feed on the epidermal layer of dry hemlock needles and may prefer this food to highly decomposed plant remains. Similarly, *Eupelops* sp. and *Peloribates* sp. will feed on parenchyma of dry leaves. Whether or not populations can subsist indefinitely on this food source is not known. A number of species, including *Scheloribates laevigatus*, *Achipteria* sp. and *Eupelops* sp. are known to feed on living green plant material (Wallwork, 1957; Woodring, 1963), although this may not be an important part of the diet under natural conditions, for reproduction apparently does not occur in cultures using this food source. However, one instance has been reported recently (Wallwork, 1965) of a galummoid mite, *Orthogalumna terebrantis* Wallw., from Uruguay feeding exclusively, at least in the nymphal stages, on living parenchyma of leaves of the water hyacinth, *Eichhornia crassipes*. The adult is active on the surface of leaves and the water surrounding the plant. The leaf is probably entered by the larva or protonymph cutting a hole in the epidermis and invading the parenchyma. A cylindrical burrow is excavated by the feeding of the three nymphal stages which develop *in situ*. After the final ecdysis the adult cuts through the epidermis and emerges. At the other extreme are species feeding only on plant material in an advanced stage of decay. These forms include the adults of many of the small species belonging to the genera *Brachychthonius*, *Oppia* and *Suctobelba*, as well as *Eniochthonius pallidulus* (C. L. Koch), *Tectocephalus velatus* and the immature stages of many of the larger species. The apparent absence of solid food in the gut of *Hypochthonius rufulus*, *Oppia* spp. and *Suctobelba* spp. may be due to these mites feeding on liquified organic material in the soil. On the other hand, many Cryptostigmata are coprophagous, particularly in the larval and nymphal stages. This habit is common among immature forms of typical wood-feeding species belonging to the genera *Steganacarus* and *Rhysotritia*, as well as in adults of *Oppia* spp., *Scheloribates laevigatus* and *Galumna formicarius* (Berl.) which are associated with these xylophages in certain situations (Wallwork, 1957). Many species feeding on liquid, semi-liquid or faecal material no doubt ingest fungal hyphae and spores associated with this material. This probably occurs in *Liochthonius* sp., *Tectocephalus velatus*, *Oppia* spp. and *Hypochthonius rufulus*. Under certain conditions *Peloribates* sp., *Hypochthonius rufulus*, *Belba* spp. and *Liochthonius* spp. have been observed to feed on carrion (Riha, 1951; Wallwork, 1957), although it is not known to what extent this forms part of the natural diet. Several instances have been given of predation by *Oribella castanea* (Herm.), *Scheloribates laevigatus* and *Galumna* sp. These appear to be isolated records, for predation is not usually associated with the slow-moving Cryptostigmata. However, it is possible that eggs of other animals, such as insects and Collembola, may provide a source of food.

A number of species, including *Scheloribates laevigatus*, *Galumna virginiensis*, *Tectocephalus velatus* and *Eupelops* sp. ingest the eggs of anoplocephalid cestodes (Rajski, 1960). Sometimes the eggs are crushed, sometimes they are swallowed whole and may continue development in the mites.

Some soil Cryptostigmata prefer woody tissue as food. These include *Mesolophora pulchra*, *Steganacarus magnus*, *Rhysotritia* spp., *Liacarus* sp., *Carabodes* sp., *Cepheus* sp., *Hermannia* sp., *Hermannella* sp., *Oppia* spp., *Scheloribates* sp. and *Galumna* sp. Decided preferences are found within this group of xylophages. Some species feed on the woody vascular elements of leaves (*Hermannia* sp., *Phthiracarus borealis*), others, such as *Mesolophora pulchra* and *Steganacarus diaphanum* Jacot consume softened, decomposing woody fibres of twigs lying on the surface of, or embedded in, the soil. A more specialized habit is shown by those mites which actually burrow into bark and heart wood of fallen twigs. *Steganacarus magnus* and *Rhysotritia ardua* may be confined to this restricted habitat in certain localities, for investigations of their burrows (Wallwork, 1957) have revealed complex formations consisting of a main channel containing the adult, and side branches occupied by immature forms. Other wood-borers are not so restricted and may spend only a part of their life cycle under these conditions as, for example, *Cepheus latus* C. L. Koch, which may become a wood-borer as an adult, although this stage is apparently not an obligate xylophage, for it may be encountered ranging freely through the soil (Wallwork, 1957). An extreme case of specialized feeding habit is provided by the mite illustrated in Fig. 4, which is tentatively identified as a tritonymph belonging in the genus *Hermannia*. It has been taken frequently from lenticels of fallen yellow birch twigs (Wallwork, 1957). All nymphal stages occur there, but no adults. Without exception, analysis showed the gut filled with corky material from the lenticel (Fig. 4). In conclusion, the distribution of three wood-borers in fallen twigs of yellow birch and hemlock is given in Table III. It may be noted from the Table that two of the three species most frequent in heart wood of yellow birch (*Steganacarus magnus* and *Rhysotritia ardua*) also occur in hemlock, but are restricted there to the bark region. This observation emphasizes the impossibility of rigidly defining the feeding habits of Acari. For most species with a wide range of habit, compensation may occur, and the emphasis on any one particular food source will vary with the soil type and locality.

In addition to these qualitative aspects of nutrition, quantitative variations during the life cycle also affect the trophic status of a species. The feeding rate of a given species may not be constant throughout the life cycle. Later immature forms may feed almost continuously, as would be expected of the growing stages, except during the pre-ecdysial quiescent periods. This point is well illustrated by Murphy and Jalil (1964) who found that 30% of the tritonymphs of *Tectocephalus velatus* had food in the gut, compared with only 17 to 22% of adults and other immatures. Studies of this kind show that feeding rate may decline sharply with age once the adult stage has been reached. This phenomenon varies with the species. Adults of *Oppia nova* and *Rostrozetes* sp. continue feeding, whereas in *Galumna elimata*, *Scheloribates laevigatus*

and *Ceratozetes cisalpinus* Berl. the feeding rate decreases considerably after a few weeks (Woodring, 1963). These considerations are of paramount importance when assessing population metabolism and community energy flow, because they emphasize the significance of the feeding habits of the later nymphal stages. Similarly, the adults of most species must be regarded as the main dispersive stage, because of their greater mobility.

The above remarks have been concerned mainly with the kinds of food material ingested by mites. The proportion of this ingested material which is assimilated and utilized for growth and energy requirements is unknown.

TABLE III
The distribution of 3 species of wood-boring Cryptostigmata in twigs
of yellow birch and hemlock undergoing wet decomposition*

Species	Yellow birch			Hemlock		
	In bark	Under bark	In heart wood	In bark	Under bark	In heart wood
<i>Steganacarus magnus</i>	+	+	+++	+++	+	-
<i>Rhysotritia ardua</i>	+	-	+	++	-	-
<i>Hermannia</i> sp. (nymph)	++	+	-	+	-	-

* High, medium and low frequencies denoted (+++), (++) and (+) respectively.

Very little information exists about the efficiency of the digestive system in the Cryptostigmata, although work has been started by Engelmann (1961) using radioactive tracers. Analyses of faecal pellets (Schuster, 1956) suggest that much of the ingested material passes out of the gut without much change in its chemical composition. Easily digested substances such as proteins, carbohydrates and lipoids are probably assimilated, but hemicelluloses, cellulose and lignin apparently are not chemically degraded by the enzyme systems of the mite. The possibility that some Cryptostigmata may possess gut symbionts that can digest these substances has been suggested (Hartenstein, 1962; Woodring, 1963), although more evidence is needed to confirm this. Another possibility is that Cryptostigmata may digest the micro-organisms on the surface of fungal hyphae, spores and plant debris, and that these materials merely act as carriers for the more digestible sources of nutriment.

V. METABOLISM

A. THE ENERGY BALANCE SHEET

The numerical abundance of the Acari in many soil types naturally leads to a consideration of their biological effects, in particular their contribution

to total soil metabolism. Here again the Cryptostigmata are singled out for special emphasis because their great numbers and feeding habits give them a certain significance in the decomposer food-chain of some soil communities. To investigate this significance it is necessary to establish not only population densities and feeding habits, but also to know how much energy is assimilated into the body, and what proportions of this assimilated energy are (1) used in metabolism, and (2) stored in the body, ultimately to be passed on to a different trophic level. The construction of an energy balance sheet of this kind is difficult, for measurements of rates of feeding, assimilation and metabolism must be made in the laboratory under controlled experimental conditions. These laboratory data have to be extrapolated to natural situations, taking account of population fluctuations and temperature variations in the habitat over a given period of time. This laboratory work presents several difficulties because the mites are so small, but with the development of special techniques for measuring rates of oxygen consumption with micro-respirometers, and rate of assimilation by radioactive tracers, considerable progress is now being made in this field (Engelmann, 1961; Macfadyen, 1963; Berthet, 1963).

The biological activity of a natural population is expressed, for purposes of comparison, in relation to the size of the population. In much purely descriptive ecological work, population size of soil mites is stated in terms of numbers of individuals. Numbers give poor estimates of the biological activity of a population in animals the size of soil mites; biomass is a much more reliable guide, and energy values per unit biomass are even more realistic. This leads to another difficulty, namely that whereas mites are not too small to be counted accurately, they are frequently too small to be weighed accurately. This difficulty may be met by assuming that most of the dry weight of the animal is in the exoskeleton, so that there is a linear relationship between dry weight and surface area of the body. Engelmann (1961) has demonstrated that this relationship is established for a number of terrestrial arthropods, and has calculated the dry weight of individual mites from the regression formula:

$$\text{Log weight } (\mu\text{g}) = 1.32 (\log \text{length} + \log \text{width } [\mu]) - 5.87.$$

The assumption on which this regression is based is evidently valid for the adults of many hard-bodied Cryptostigmata, but the relationship may be less direct for gravid females of some of the larger species (which may contain as many as 20 mature or nearly mature eggs) and immature forms, particularly tritonymphs where, theoretically at least, dry weight may be more a function of volume than of surface area. Furthermore, in using this method to calculate metabolism it must also be assumed that the exoskeleton is metabolically active (F. Raw, personal communication), and this may not be true in adult Cryptostigmata.

The amount of food assimilated by an organism in a given period of time can be determined if the amounts consumed and egested are known. The amount of food consumed under natural conditions is difficult to measure

and is obviously affected by a number of variables including, for Cryptostigmata, moisture content of food, its state of decomposition and environmental temperature. An indirect method of estimating consumption has been suggested by van der Drift (1951) from studies on the feeding rates of the diplopod *Glomeris marginata*. This method is based on the assumption that there is a definite relationship between feeding rate and body weight so that:

$$\text{Food consumed} = \sqrt[3]{(\text{body weight})^2} \times \text{constant.}$$

According to this relationship the relative feeding rate (i.e. feeding rate per unit weight) decreases with increasing body weight. Evidence from feeding studies on Cryptostigmata indicates that the relative feeding rate decreases with increasing body weight and that the absolute feeding rate of the nymphal forms, particularly the tritonymphs, is higher than that of the adults. This would affect the constancy of the above relationship. Balogh (1958) has discussed other limitations of the method. On the other hand, the direct weighing method using differences in weights ingested and egested as estimates of assimilation is also subject to errors because of the small amounts of materials involved. Engelmann (1961) obtained more reliable estimates of assimilation by using yeast labelled with radioactive glycine ^{14}C as the food source. He calculated that the food assimilated by the Cryptostigmata of a grassland soil was equivalent to 8% of their body weight per day; expressed in terms of the whole population (biomass: 54 mg/m²) for one year, this amounted to about 20% of the food ingested.

The next item on the balance sheet, metabolic estimates, can be calculated by indirect or direct methods. Engelmann (1961) calculated respiration rates of several species of Cryptostigmata indirectly, where technical difficulties prevented direct estimations. The method assumed a linear relationship between log body weight and log respiration which, for the data used, could be expressed by the equation:

$$\text{Log respiration } (\mu\text{l } 10^{-3}) = 0.85 (\log \text{weight in } \mu\text{g}) + 0.44.$$

By using the results obtained by this regression technique in conjunction with direct respirometric estimates made at 25°C, and by correcting them for temperature conditions of the habitat, Engelmann calculated that the yearly expenditure of energy on respiration by the whole population under natural conditions was about 96% of the total energy assimilated into the body during that period.

Respiration rates can be used as a reliable index of metabolic activity. When combined with calorimetric studies, they provide a basis for comparing the contribution of individual trophic groups to total soil metabolism. For detritus-feeding forms, such comparisons help to explain their importance in decomposition processes. Despite the variability in the results obtained by direct respirometry, this approach promises to be more reliable than the indirect method. Berthet (1963) determined the oxygen consumption of several species of Cryptostigmata from a forest soil. Although results for

individuals of the same species differed greatly, he was able to demonstrate the influence of temperature and body weight on respiration rate. Thus, oxygen consumption of *Platynothrus peltifer* and *Parachipteria willmanni* remained relatively constant at 15°C and was 0.222 mm³ and 0.176 mm³ respectively per individual per day. Measurements at different temperatures indicated a linear relationship between the log oxygen consumed and temperature which only held within the range 5–15°C. Above this range, the oxygen consumption was lower than expected and the relationship assumed a sigmoid form. This characteristic was apparently not taken into consideration by Engelmann. Within the range 5–15°C a relatively constant temperature coefficient of approximately 4 was calculated for 16 common species. An exponential relationship between body weight and oxygen consumption was described for individuals of *Steganacarus magnus* at 15°C, and as a result of these studies Berthet postulated a general relationship between oxygen consumption, temperature and body weight, expressed by the equation:

$$Y = 18.059 + 0.7W - 0.487Z$$

where $Y = \log$ oxygen consumed/individual/day in 10^{-3} mm³

$W = \log$ body weight in µg and

$$Z = \frac{1}{T_{abs}} \cdot 10^4$$

Methods such as these can be extended to determine energy flow and transfer within and between different trophic levels in the soil community. Without data on differential mortality rates, the efficiency of energy transfer from one level to another must be based on assumptions until further developments provide more precise estimates. The preceding discussion has been concerned exclusively with the energetics of the decomposer level, for it is with this level that the very large majority of soil Acari are identified. The little work done on the energy relations of predatory mites by Engelmann (1961) and Macfadyen (1963) indicates that these forms may make a significant contribution to energy circulation in the community. A detailed energy balance sheet cannot be given for the Cryptostigmata at present, although the results surveyed briefly above do give indications of the picture emerging from these studies. It seems that much of the energy ingested is not assimilated into the body, but is egested with the faeces. Thus, the Cryptostigmata are wasteful feeders from this point of view (Macfadyen, 1963). Much of the energy assimilated into the body is used in respiration and only a relatively small amount is incorporated into the standing crop biomass.

B. THE DECOMPOSER FOOD CHAIN

Finally we turn to the role of the acarine decomposers in breakdown processes occurring in the soil. The overwhelming importance of decomposers in some situations has been demonstrated by Macfadyen (1963), who calculated that this group attracted considerably more of the energy flow than the

herbivore/carnivore food chain in a meadow soil. There is further evidence that the decomposer fraction is well represented in a variety of soil types, although the small-sized decomposers, of which the *Cryptostigmata* form a prominent part, predominate in mor-type soils (Macfadyen, 1963). *Cryptostigmata* have a low metabolic rate compared with other small-sized decomposers such as *Collembola*. Berthet (1963) calculated that the metabolism of these mites accounts for only 1·8% per annum of the total soil metabolism in a forest soil. He also found that the mites of the litter layer, although fewer and having a smaller biomass than those in the lower organic layers, made an appreciably greater contribution to soil metabolism than the latter, a fact he attributed to higher respiration rates of litter inhabitants during the summer months.

The impression gained from these quantitative studies is that the *Cryptostigmata* play only a minor role in the direct decomposition and chemical degradation of litter material. It is clear from the results of feeding studies that most of the detritus-feeding *Acari* prefer decomposing plant material or fungi. Their contribution to primary breakdown of fresh litter may be studied using the litter-bag technique, in which litter is contained in bags of varying mesh sizes to exclude certain faunal groups, and then placed on the surface of, or embedded in, the soil. Using this approach, Edwards and Heath (1963) and van der Drift (1963) concluded that the *Cryptostigmata* are of little importance in primary decomposition. On the other hand, Crossley and Witkamp (1964) were able to demonstrate a successional development of the mites in litter bags, characterized by an initial invasion by large numbers of individuals belonging to a small number of species, followed by an increase in species diversity as decomposition proceeded, and a reduction in the number of individuals per species. Most *Cryptostigmata* would seem to be associated more with the later stages of decomposition, and even here their effect appears to be small. Before making any final assessment, however, there are two important points to be borne in mind. First, most determinations of metabolic rate and food assimilation have been made on adult mites. Now the nymphal stages, at least of the *Cryptostigmata*, appear to be the important feeding stages in the life cycle, and it is possible that they have a higher metabolic rate than the adults. These weakly chitinized immatures are also more vulnerable to predators, and may participate more than the adults in the transfer of material and energy to higher trophic levels in the community. When more information is available about the biological activity of these immature forms, the assessment of the metabolic contribution of the *Cryptostigmata* to total soil processes may well need revision. Berthet (1963) has shown that nymphal *Cryptostigmata* may contribute as much as 70% to the total metabolism of the whole group during a year. Second, the long-term metabolic role of these mites must be considered. Many forest soils provide unsuitable conditions for the larger and metabolically more active decomposers, and under such conditions the slow but continuous decomposition of plant material may be maintained appreciably by the activity of detritus-feeding mites. However, we know little of these long-term effects

in which soil micro-organisms such as Protozoa and bacteria may also be important.

On the other hand, many authors have stressed the indirect importance of the detritus-feeding mites in litter decomposition. In many ways, that cannot be determined quantitatively at present, these mites assist the decomposition processes by promoting the growth and distribution of micro-organisms (see Fig. 6) and fungi (Fig. 3), and by transporting the products of decomposition to the lower layers and root zones of the soil profile. The relationship between the mites and fungi is complex. Some forest soils having dense fungal mats do not support large populations of Cryptostigmata, which suggests antagonism between the two groups of organisms, although it may result from differential reaction to some environmental factor such as low relative humidity. In other situations, the feeding of fungivorous mites may control the growth of fungi and may lead ultimately to more vigorous fungal growth, by preventing overcrowding. Mites play an important part in the dissemination of fungal spores, which may adhere readily to the surface of the body or be transported in the gut of the mites. Xylophagous species may be particularly important in this respect. Although the symbiotic relationship between mites and micro-organisms requires confirmation, the two groups may be associated in the decomposition process, for there is evidence that litter or decomposing material may be more susceptible to microbial activity after it has passed through the gut of the mites (Ghilarov, 1963; Kühnelt, 1963). The "wasteful" feeding behaviour of the Cryptostigmata may in fact be quite the reverse (Macfadyen, 1961). The comminution of organic material by their mouthparts may be important in the physical breakdown of litter, thus exposing a greater surface area to microbial activity and leaching (Crossley and Witkamp, 1964). The importance of the Cryptostigmata in the transportation of organic material in an advanced stage of decay to deeper layers of the soil profile is established from identification of characteristic faecal pellets. A study by Jongerius (1963) on the humus components of three different profiles defines this activity in quantitative terms. According to these findings, the Cryptostigmata play a more prominent part in the vertical transportation of organic material in a mor profile than in a mull type and, in the former, the volume of mite excrements is appreciable in the root zone at a depth of 7 to 12 cm, whereas the excrements of larger decomposers are localized in the upper regions of the profile. The Cryptostigmata appear then to be important in the deep mixing of organic material. In contrast, the larger decomposers are more effective in surface mixing.

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